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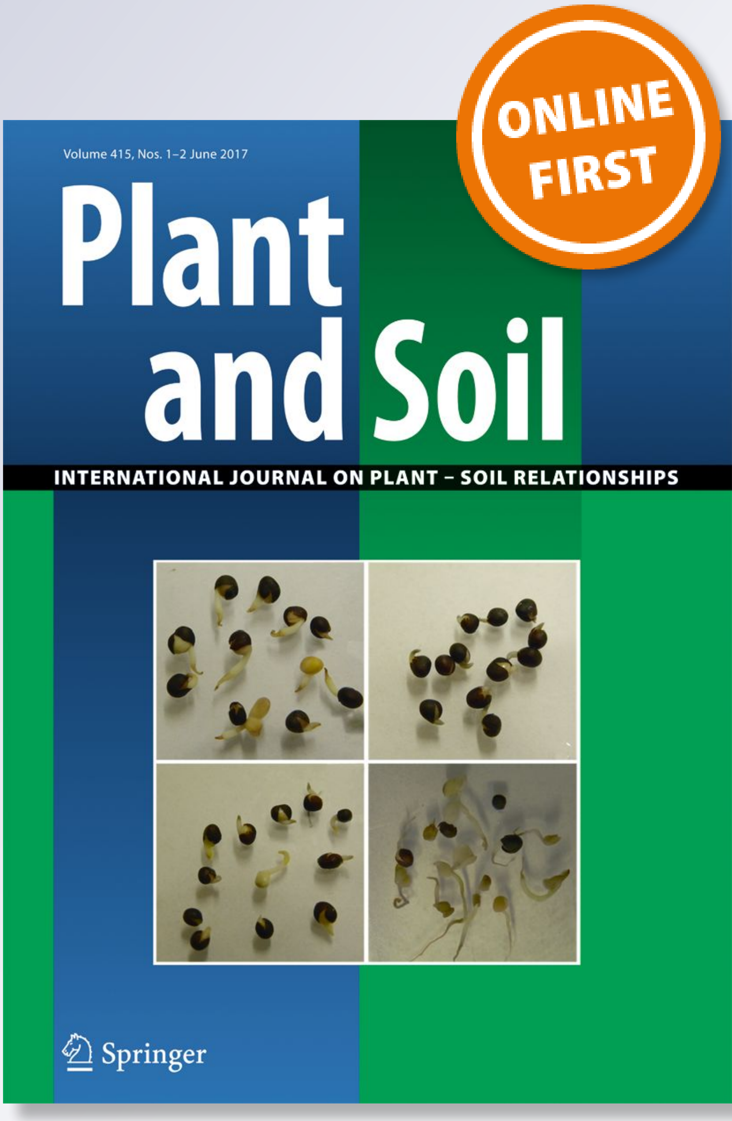

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REGULAR ARTICLE

Leaf habit of tree species does not strongly predict leaf litter decomposition but alters climate-decomposition relationships

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Abstract
Aims Leaf habit of tree species (evergreen versus deciduous) is proposed to be an important determinant of leaf litter decomposition, but it remains largely understudied as to how climatic regulation of litter decomposition differs between leaf habits.
Methods We isolated the relative role of climate and leaf habit in leaf litter decomposition by investigating the latitudinal pattern of leaf litter decomposition for Chinese broad-leaved tree species.
Results Litter decomposition rate decreased with latitude, which was largely driven by mean annual temperature (MAT). Evergreen and deciduous broad-leaved tree species shared similar decomposition rate where they coexisted. Leaf litter decomposition of evergreen broad-leaved tree species was more sensitive to MAT than that of the deciduous species, whereas leaf litter decomposition of the deciduous trees was more sensitive than that of the evergreen to mean annual precipitation. Climatic variables explained more variation in leaf litter decomposition than did leaf habit alone.
Conclusions Our findings support the conventional paradigm that climate is a dominant regulator of leaf litter decomposition over broad geographical scales, notwithstanding recent studies calling into question this paradigm. While leaf habit alone does not predict leaf litter decomposition very well where both evergreen and deciduous species coexisted, the direction and strength of shift in leaf litter decomposition diverged between leaf habits across the climatic gradient. These findings underscore the urgent need to consider the impacts of changes in leaf habits when predicting leaf litter decomposition in response to climate change.

Keywords Evergreenness · Mean annual temperature · Nutrient cycling · Leaf life span · Broad-leaved forests ecosystems

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Introduction

Leaf litter decomposition is one of the key cogs in the gear of forest ecosystem functioning (Berg 2014; Cleveland et al. 2011; Handa et al. 2014). Decomposition of leaf litter refers to the physical, chemical, and biological processes that are involved in emission and storage of carbon (C), nutrient release, as well as the formation of humus substances in the soil. As such, it is a critical ecological process in the formation of soil organic matter, the mineralization of organic nutrients, as well as maintenance of the carbon balance in forest

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ecosystems (Berger et al. 2015; Hobbie 2015; Wieder et al. 2009). Furthermore, changes in the rates of decomposition have profound effects on ecological functioning such as ecosystem productivity, particularly in forest ecosystems where nutrient supply is predominantly controlled by decomposition and mineralization of leaf litter (Cusack et al. 2009; Marklein et al. 2016; Taylor et al. 2017). Altered patterns of temperature and precipitation induced by ongoing climate change will affect the turnover of leaf litter and consequently alter carbon storage. Therefore, it is very essential to understand the general mechanisms underlying the decomposition process in order to accurately quantify biologically driven C and nutrient fluxes under climate change scenario (Aerts et al. 2012; García-Palacios et al. 2016; Keiser and Bradford 2017).

There is a complex and interacting set of factors that simultaneously control leaf litter decomposition, such as climate, leaf litter quality and their interactions. Climate, usually incorporating temperature and precipitation, is traditionally viewed as the predominant regulator of decomposition rates of leaf litter at global and regional scales (Aerts 1997; Alessandro and Nyman 2017; Currie et al. 2010; Taylor et al. 2017). Existing studies on the tropical, temperate, and boreal forests have found that increased temperature or precipitation could accelerate litter decomposition (Keiser and Bradford 2017; Prescott 2010; Salinas et al. 2011). However, other empirical studies have indicated that climate is a less important determinant of leaf litter decomposition than other local factors, such as plant litter traits across broad-scale geographical gradients (Cornwell et al. 2008; Zhang et al. 2008). Moreover, a more recent effort conducted by Bradford et al. (2016) by reanalyzing previous litter decomposition data have demonstrated that climate failed to predict leaf litter decomposition due to large variation of litter decomposition at the individual sites and questioned the long-standing assumption that climate is the predominant regulator of leaf litter decomposition at large scales. This has suggested that factors other than climate could govern leaf litter decomposition. Therefore, our understanding of the extent of climate control on litter decomposition remains relatively limited, given the fact that the roles of climate could vary across the different regions (Berg 2014; Cleveland et al. 2011; Ge et al. 2017).

Another potentially important regulator of leaf litter decomposition is leaf litter quality (Aerts 1997; Freschet et al. 2013; Pietsch et al. 2014). Empirical studies have shown that litter quality generally defines how beneficial the litter is to the decomposer organisms as the major common source of energy or nutrients and thus should be a secondary determinant of leaf litter decomposition rate, and various descriptors of litter quality significantly correlate with leaf litter decomposition (Hättenschwiler et al. 2011; Zanne et al. 2015). For example, litter nitrogen and lignin concentrations have been identified as indicators of litter quality due to their effects on microbial activities and litter decomposition rates (García-Palacios et al. 2013; Ge et al. 2017).

Despite considerable effort, no consistent single litter-quality index has been acquired (Aerts 1997; Portillo-Estrada et al. 2016; Prescott 2010). Leaf habit of tree species (evergreen versus deciduous) could structure the leaf economics spectrum very well (Pringle et al. 2011; Zhao et al. 2017), which is tightly linked to leaf litter quality and thus to litter decomposition (Freschet et al. 2012; Pietsch et al. 2014; Wright et al. 2004). Thus, we infer that leaf habit of species, based on the observation of different traits, may have the potential to provide alternative proxy information on suites of leaf litter traits that drive leaf litter decomposition (Cornelissen et al. 1999; Powers and Tiffin 2010; Verheijen et al. 2016). Existing studies have suggested that litter decomposition of evergreens is slower than that of the deciduous species, and thus leaf habit may be a good predictor of leaf litter decomposition rate (Aerts and Chapin 1999; Dorrepaal et al. 2005). However, the robust evidence of leaf habit effect on leaf litter decomposition is relatively lacking, since our understanding of leaf habit effect on leaf decomposition arises from only a few taxa within a limited geographical area, with less-studied broad-leaved forests (Ge et al. 2017; Huang et al. 2007; Liu et al. 2016). Moreover, clarifying leaf habit effect on litter decomposition also has important implications for the ability of earth system models to accurately couple the carbon and nitrogen cycles since most of such models rely mainly on parameterization of plant functional types defined partly by leaf habit (Berg et al. 2015; Bohlman 2010; Hobbie 2015). The potential for leaf habit is particularly attractive since data on leaf habit are fairly easy to collect through remote sensing technique and could serve as the indictor of species composition shifts in broad-leaved forests in response to climate change (Lu et al. 2017; Ouédraogo et al. 2016; Singh and Kushwaha 2016).

While many studies have provided great insight into how climate and leaf habit affects leaf litter decomposition, the relative role of climate versus leaf habit in driving leaf litter decomposition has received less attention and is still a matter of debate, which is particularly dependent on the constraining factors in the studied environments. Indeed, a direct comparison of variance contributed by each of these selected predictors has not been examined due to study approaches or dataset limitations (Dorrepaal et al. 2005; Ge et al. 2017; Waring 2012). If leaf litter decomposition can be modeled as a function of leaf habit and climate, this would greatly simplify the way in which we can predict the biogeochemical consequences of shifts in species composition caused by climate change (Cornwell et al. 2008; Hobbie 2015; Powers and Tiffin 2010; Verheijen et al. 2016). However, most studies on this topic have been conducted in a single site or by using few species of leaf litters (Cornelissen et al. 1999; Liu et al. 2016). Moreover, the extrapolation of leaf habit effect on leaf litter decomposition under different climatic conditions existing in the published papers is often difficult since researchers can only focus on one climatic driver in their study. Nonetheless, this limitation can be overcome by analyzing the results from syntheses of multiple published studies conducted at a single site.

The eastern region of China is characterized by large temperature and precipitation gradients. Evergreen and deciduous broad-leaved tree species constitute a large proportion of the tropical, subtropical and temperate forests in this region and play a fundamental role in carbon cycling (Ge et al. 2015; Wu 1980). The prominence of evergreen broad-leaved tree species decreases as the latitude increases, while deciduous broad-leaved tree species display the opposite trend across this gradient. Such shift in prevalence between evergreen and deciduous species represents a potentially substantial change in ecosystem functional properties, including litter decomposition. This unique region provides an exceptional model system to assess the linkage between leaf litter decomposition for different leaf habits of tree species and climate factors (Ge and Xie 2017a). Most importantly, the regulation of leaf litter decomposition of evergreen and deciduous broad-leaved trees by different climate variables may have profound consequences for carbon and nutrient cycling and other associated ecological processes.

Here, we conducted a large-scale study of leaf litter decomposition of broad-leaved tree species in forest ecosystems across eastern China, which have been greatly under-represented in prior meta-analyses (Cornwell et al. 2008; Waring 2012; Zhang et al. 2008). We did that by developing a comprehensive database that synthesized previous published studies and our additional sampling in eastern China with large taxonomic and geographical coverage. Specifically, we aimed to: (1) examine leaf litter decomposition rates between leaf habits, (2) rigorously evaluate the relationships between climate and leaf litter decomposition rates, and (3) explicitly parse the relative contribution of climate and leaf habit to variation in leaf litter decomposition. Understanding how leaf habits of tree species adjust their decomposition rate to climate may well enable us to quantify climate-driven litter nutrient feedback to soils and infer the effects of ongoing climate changes on nutrient cycling of broad-leaved forests.

Methods

Data collection and processing

We conducted a regional meta-analysis of published studies and our additional sampling data for the leaf litter decomposition constant k (single exponential), and associated coefficient of determination (R^2) of broad-leaved tree leaves in China. We also collected ancillary site information such as geographical location, mean annual temperature (MAT), and mean annual precipitation (MAP) (See **Appendix S1** for data sources and the complete list of references). We critically reviewed all sources of data and followed specific criteria in order to filter the data we included in our updated database. First, we only kept data for in-situ leaf litter decomposition of single tree species regarding the possible effects of home-field advantage and excluded the experiments performed in laboratory to ensure high levels of comparability of climate variables. Second, the decomposition constant k was derived from measurements obtained for longer time than one year. Third, we only utilized the data collected from the soil surface litterbags method, where the mesh size ranged from 0.5 mm to 2 mm. We rejected the data from fertilized stands and introduced tree species. We also added our unpublished dataset into this database. The total variation in accumulated mass loss for the used data ranged from 30.2 to 71.6% for evergreen and 43.2 to 76.4% for deciduous litter.

We calculated the decomposition constant k by a first-order exponential decay function similarly to previous studies (Olson 1963) where leaf litter mass loss was reported. In most publications, the decomposition constant, k, and coefficient of determination (R^2) of the model were reported, and these values were incorporated into our database directly.

Approximately 7% of the total dataset lacked climate variables MAT and MAP, thus we extracted these variables from a global climate database at the highest resolution (30 arc-seconds) (http://www.worldclimate.org) (Hijmans et al. 2005) and inferred MAT and MAP using geographical location. In order to test the accuracy of the inferred climate data, we also used the climate data of the sites that contained original climate variables, and correlated the inferred climate values with known values. The results indicated high positive correlations between our collected and inferred data (r = 0.94), highlighting that the latter was a robust estimator of climate effects on leaf litter decomposition. Hence, we used inferred climate data as a surrogate to represent the climate information of sample sites where no climate data had been reported. The relationship between MAT and MAP across our studied region was positively correlated ($p < 0.05$) (See **Appendix S2**). In total, we collected 413 observations of leaf litter decomposition k values for 134 tree species at 63 sites. Site MAT ranged from −3.3 °C to 24.9 °C and MAP from 489 mm to 2651 mm.

Data analysis

We analyzed the data at two levels: (1) we used all of the data collectively; and (2) we classified the dataset into two leaf-habits: the evergreen and the deciduous species based on the Flora of China. Data on leaf-litter decomposition (k value) exhibited significant heteroscedasticity and non-normality. Thus, we transformed this variable using natural logarithm to meet normality and homogeneity assumptions for regression analysis and analysis of variance, as is commonly done in previous studies (Han et al. 2011; Ordoñez et al. 2009; Reich et al. 2007). To examine the relationships between the estimated k values and climate variables, we conducted multiple regression analysis to identify the overall patterns of leaf litter decomposition in relation to MAT and MAP. We then examined the effects of climatic variables (MAT and MAP) and leaf habit (evergreen versus deciduous).

Considering that regional-scale modeling and vegetation function may be confined to functional groups, such as leaf habit, it was important to compare the data at this level of classification (Dorrepaal et al. 2005; Han et al. 2011; Woodward et al. 2004). Such comparisons enable us to determine how evergreen and deciduous species differ in their responses to climatic drivers of leaf litter decomposition. We firstly compared the means of each leaf habit using one-way analysis of variance (ANOVA). The result can be found in **Appendix S4**. Regarding the control of climate on the geographical distribution of evergreen and deciduous broad-leaved tree species (Ge and Xie 2017a; Wu 1980), we also extracted these data in sites where the evergreen and deciduous broad-leaved tree species coexisted and used paired t-tests to detect pure leaf habit effect on litter decomposition rate with similar climates. We further tested how the specific responses of leaf litter decomposition to MAT and MAP differed between leaf habits using multiple linear regressions. Specifically, we used litter decomposition rate k value as response variable and climatic variable (MAT and MAP as continuous variables) and leaf habit (categorical variable) as independent variables. The statistical method has followed prior studies (Chen et al. 2013; Han et al. 2011; Ordoñez et al. 2009; Ouédraogo et al. 2016). Given the strong collinearity between MAT and MAP that may influence the confidence interval for our model parameter, we also conducted partial least-squares regression (PLS) to be sure that our statistical conclusions are robust. This method could allow for the direct comparison of the regression parameters of different predictor variables. Compared to multiple linear regressions, PLS model could effectively construct a multiple linear relationship between dependent and independent variables if these independent variables are highly correlated (Geladi and Kowalski 1986; Haenlein and Kaplan 2004; Wold et al. 1984). We found similar results and could verify our conclusions. To facilitate the understanding of our statistical results, we only present the results of multiple linear regressions. However, regarding fewer sites and narrower climatic ranges, we did not check statistical differences between leaf habit in response to climatic variables where both evergreen and deciduous species coexisted.

To evaluate the relative importance of climate and leaf habit in shaping the geographical pattern of leaf litter decomposition, we conducted a variation partitioning analysis following previous studies (Ray-Mukherjee et al. 2014). We determined significant differences for all statistical tests when p value was equal to or less than 0.05. We performed all statistical analysis in R 3.0.0 (R Core Team 2013).

Results

Statistics of leaf litter decomposition across Chinese broad-leaved tree species

Our dataset was geographically comprehensive, including many sites that covered a wide distribution of broad-leaved tree species across subtropical and temperate regions. Leaf litter decomposition rates varied considerably within and among sites. The leaf litter decomposition constant k ranged from 0.08 to 4.34 year^{-1} across broad-leaved tree species, and had an average of 0.77 year^{-1}. The majority of k values (76%) were distributed in a range of 0–1.00 (Fig. 1a). Moreover, these k values were well estimated by the fitted first-order exponential decay function and R^2 for 89% of species was >0.8 in this study (Fig. 1b).

Leaf litter decomposition between leaf habits

Across our studied region, the mean k value of evergreen broad-leaved species was 0.943 year^{-1}, which was statistically higher than that of the deciduous counterparts (0.598 year^{-1}) ($p < 0.05$). However, the k value within both leaf habits showed high variability (Fig. 2a). When our data set was restricted to sites where evergreen and deciduous broad-leaved tree species coexisted to exclude the confounding effects of environment, leaf habit effects on leaf litter decomposition was not significant (paired t-tests, $p > 0.05$) (Fig. 2b).

Leaf litter decomposition across the climate gradient

The leaf litter decomposition rate k value correlated well with climate metrics (MAT and MAP) (Fig. 3). For all species pooled together, the k value correlated positively with MAT ($p < 0.05$). Similarly, the k value increased from low to high MAP, but not significantly ($p > 0.05$).

Moreover, we found that the leaf litter decomposition k value of evergreen and deciduous broad-leaved species responded significantly to MAT and MAP; however, the slopes of these relationships differed between leaf habits, as indicated by the significant interactions between leaf habit and climatic variables (**Appendix** S4). We found that decomposition rate of evergreen broad-leaved tree species responded faster to MAT than that of the deciduous species, whereas decomposition rates of the deciduous trees responded faster than that of the evergreen to MAP (Fig. 4 and **Appendix** S5).

Relative importance of climate and leaf habit in leaf litter decomposition

Interestingly, MAT was the most important factor in shaping the biogeography of leaf litter decomposition rate. A general linear model analysis indicated that climate factors and leaf habit together accounted for 26.75% of geographical variation in leaf litter decomposition rates (Fig. 5). The individual effect of MAT (6.77%) was much higher than that of both MAP (0.38%) and leaf habit (0.07%). The ranking of total effects of MAT, MAP and leaf habit on leaf litter decomposition rates was as follows: MAT (26.37%) > MAP (19.63%) > leaf habit (11.69%).

Discussion

To the best of our knowledge, this is the first attempt to comprehensively identify and quantify large-scale

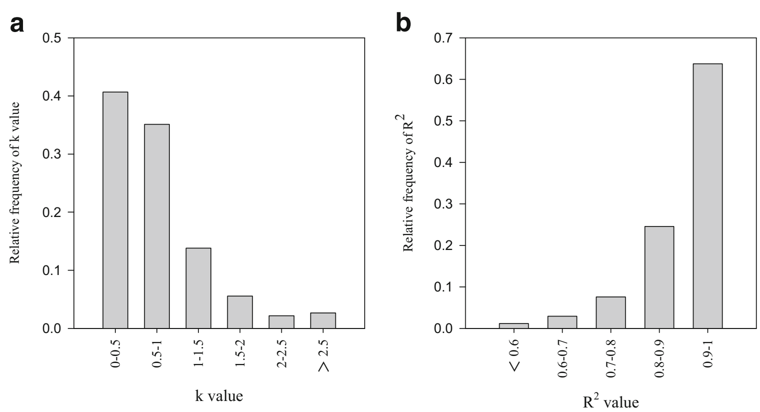

Fig. 1 Relative frequency of k value (**a**) and coefficient of determination R^2 (**b**) for decomposition studies in Chinese broad-leaved tree species

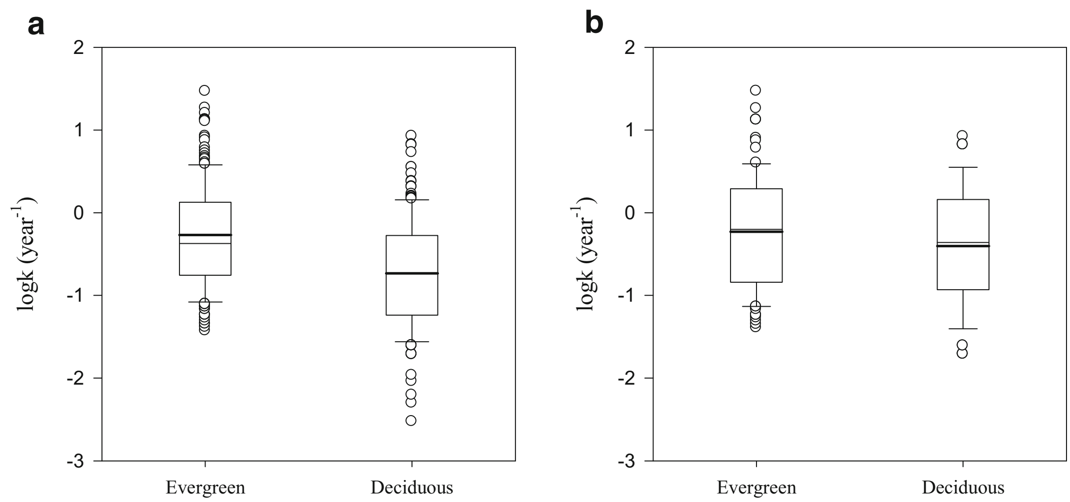

Fig. 2 Comparisons of leaf litter decomposition k value between Chinese evergreen and deciduous broad-leaved tree species. **a**: across the entire data set ($p < 0.05$). **b**: only including the dataset at sites where both leaf habits coexisted ($p > 0.05$)

variation in leaf litter decomposition with the geographically most representative broad-leaved tree species in China. Our study complemented previous specific-ecosystem studies on litter decomposition rate at the global scale (Aerts 1997; Zhang et al. 2008) and extended the results of earlier site-specific and regional-scale studies (Ge et al. 2017; Huang et al. 2007; Liu et al. 2016; Zhou et al. 2008), thus providing further new details such as regional mean and variation of leaf litter decomposition rate for broad-leaved forest ecosystems. For example, in comparison with Zhang et al. (2008) and Zhou et al. (2008), this study has synthesized more recently published data on Chinese broad-leaved tree species, which reflect the most recent understanding of litter decomposition process. Our study has further addressed the interactive effects of climate and leaf habit on leaf litter decomposition. Therefore, our present analysis could advance our understanding of how climate and leaf habit interactively influence the geographical pattern of leaf litter decomposition rates and consequently biogeochemical cycling in broad-leaved forest ecosystems.

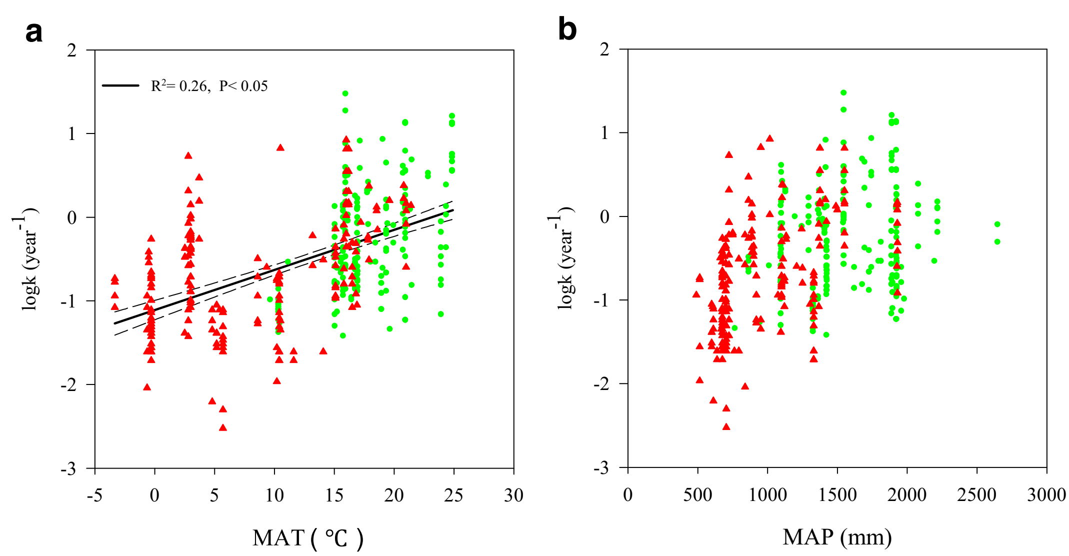

Fig. 3 Variation of leaf litter decomposition k value in relation to MAT (**a**) and MAP (**b**) in Chinese broad-leaved tree species. Green circles and red triangles represent data points for evergreen and deciduous species, respectively. Regression lines were plotted for relationships with $p < 0.05$

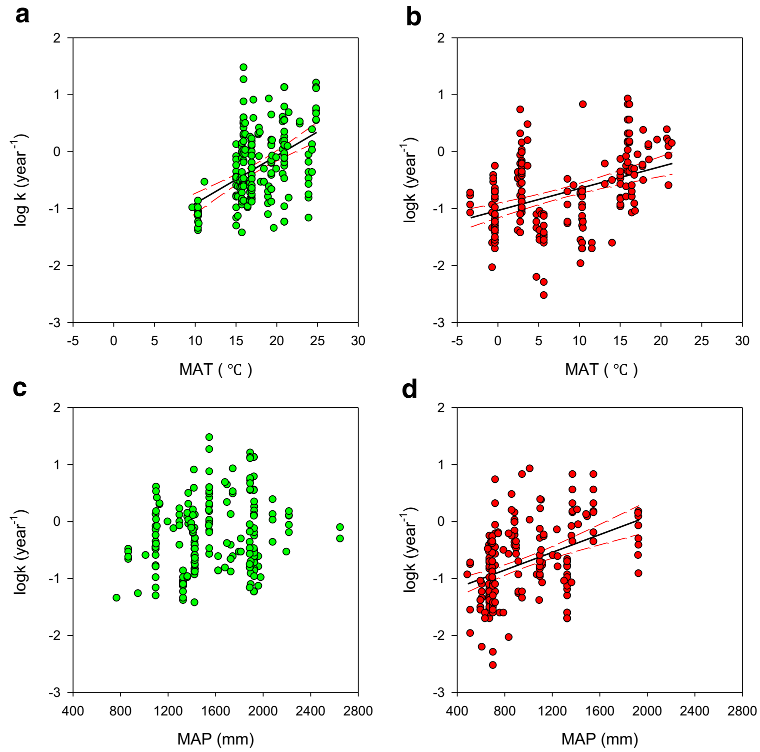

Fig. 4 Relationships between litter decomposition and climatic variables for evergreen and deciduous broad-leaved tree species. Green circles and red triangles represent data points for evergreen and deciduous species, respectively. Regression lines were plotted for relationships with $p < 0.05$. Solid lines indicate the model-fitted values and dash lines represent 95% confidence intervals. For easier comparison of the relationships between leaf habits, the model-fitted values were also shown in **Appendix** S6

Leaf litter decomposition falls into global-scale range and shows high variability

Across Chinese broad-leaved tree species, the overall mean k value of leaf litter decomposition obtained here (0.77 year^{-1}) indicated that the mean residence time of leaf litter (1/k) is no more than two years. Not surprisingly, this rate is similar to the reported value for global broad-leaved forests (Zhang et al. 2008). Moreover, this rate is within the range of global litter decomposition rates (Aerts 1997; Zhang et al. 2008), yet slightly higher than values reported for temperate ecosystems (Aerts 1997; Freschet et al. 2013; Ge et al. 2017) and much lower than the mean value in tropical regions (Powers et al. 2009; Waring 2012; Wieder et al. 2009). In this study, 89% of R^2 values were higher than 0.8, indicating that most leaf litter decomposition data can be accurately estimated by the first-order exponential decay function for these forests, a finding consistent with other studies (Gholz et al. 2000; Zhang et al. 2008).

On average our study demonstrated that the Chinese broad-leaved tree species have a large variation in leaf-litter decomposition rates (**Appendix S3**), suggesting that a wide range in decomposition rate is a common feature of Chinese broad-leaved tree species. Not surprisingly, this broad latitudinal variation in the estimated k value was largely attributable to the factors we have investigated here including geographical locations, climate conditions, and leaf habit (**Appendix S4**).

Leaf litter decomposition is more sensitive to temperature than precipitation for all tree species

Here, we found a positive relationship between k value and MAT. This agrees well with previous studies in temperate and boreal forests (Makkonen et al. 2012), and indicates that favorable temperature conditions stimulate the activity of the decomposition by fungi and soil fauna and accelerate leaf litter decomposition (Cleveland et al. 2011; Zhou et al. 2008). Our empirical analysis further showed that an increase in MAT by 1 °C would result in a 4.8% (the standard error is 0.01) increase in the k value for Chinese broad-leaved tree species, significantly higher than the previously estimated value at the global scale (i.e. ca. 2.9%; this global value was primarily estimated from Zhang and Wang 2015). Besides, our study showed that the k value also increased with MAP, but not significantly, when considering the strong correlation between MAT and MAP. This result is in contrast to that for tropical forests (Powers et al. 2009; Waring 2012; Wieder et al. 2009)**,** but

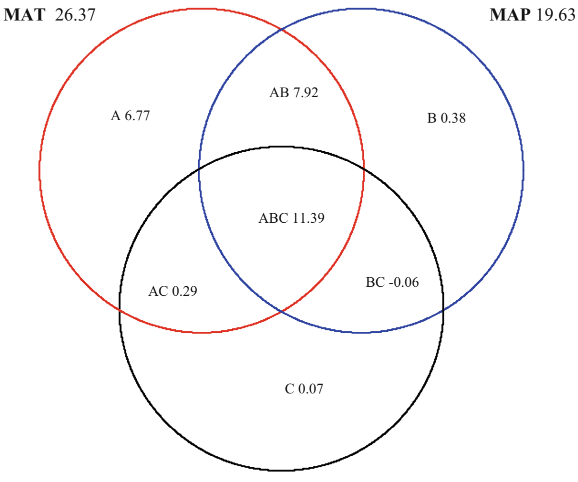

Fig. 5 Variation partitioning of climate and leaf habit in accounting for variation in leaf litter decomposition rate in Chinese broad-leaved tree species. The symbols A, B, C represent the unique effects of MAT, MAP and leaf habit, respectively; AB is the interactive effect of MAT and MAP; AC, the interactive effect of MAT and leaf habit, BC, the interactive effect of MAP and leaf habit, and ABC, the interactive effect of MAT,MAP and leaf habit

similar to those for temperate and boreal forests (Currie et al. 2010; Portillo-Estrada et al. 2016) and global terrestrial ecosystems (Zhang and Wang 2015). Further, our results did not support the conclusion in the earlier work of the Long-Term Inter-site Decomposition Experiment in China (LTIDE-China), which observed that MAP could play a secondary role (Zhou et al. 2008). Therefore, we argue that there is a more pronounced temperature sensitivity of leaf litter decomposition for broad-leaved tree species than assumed by previous global estimate regardless of other environmental factors. The wider range of MAT relative to MAP can make MAT a better predictor of decomposition across Chinese broad-leaved tree species. Specifically, in our study, most of the k values were derived from the eastern region of China where precipitation was relatively abundant and temperature thus could be the rate-limiting factor. Correspondingly, there are very few forests in China where the annual precipitation is less than 500 mm (Wu 1980). Moreover, in our study the range of MAT was much wider than that of MAP. Thus, MAT evidently overshadows any effect of MAP and contributes more to latitudinal variation in k values of Chinese broad-leaved tree species. These detected relationships between climatic variables and decomposition rate may be useful in efforts to model decomposition rates across broad-leaved forests ecosystems.

Leaf habit alone does not strongly predict leaf litter decomposition very well

Leaf habit effect on litter decomposition has been somewhat equivocal in previous studies (Cornelissen et al. 1999; Cornwell et al. 2008; Liu et al. 2016). Some studies that have identified leaf habit effect on litter decomposition were generally confounded with environmental effects (Augusto et al. 2015; Huang et al. 2007). In our study, we compared differences in litter decomposition rates between evergreen and deciduous species by restricting our data to sites where evergreen and deciduous co-occurred to exclude environmental effects. The lack of evidence for leaf habit predicting leaf litter decomposition within the Eastern Chinese region observed here is consistent with those measured in the Mediterranean region, but contrasted to reports for both temperate and tropical regions (Aerts and Chapin 1999). Besides, this conclusion did not support the earlier viewpoint that litter from deciduous species decomposed 60% faster than that from evergreen species at the global scale (Cornwell et al. 2008). These inconsistent leaf habit effects on decomposition rates among the above-mentioned studies indicate that leaf litter decomposition is ecosystem-dependent and is influenced by too many various litter traits to be well captured by leaf habit alone. Our results imply that a plant functional type classification based on leaf habit alone has little utility to predict leaf litter decomposition and associated ecosystem functioning in broad-leaved forests.

There are likely many potentially plausible reasons for the similarity of evergreen and deciduous decomposition rates with a common environmental regime. For one, deciduous species studied here may comprise the same leaf litter traits as evergreen broad-leaved tree species that contribute to leaf litter decomposition (Aerts and Chapin 1999; Ge et al. 2016; Huang et al. 2007). Another likely candidate may arise from the differential effects of various leaf litter traits on litter decomposition (Dias et al. 2017; Hobbie 2015; Powers and Tiffin 2010). Previous studies indicate that leaf litter decomposition is strongly linked to various indicators of leaf litter traits (Chomel et al. 2016; Hättenschwiler et al. 2011). For example, leaf litter nitrogen (N) in evergreen species was higher than that in deciduous species but leaf litter phosphorus (P) displayed the opposite trend (Cornelissen et al. 1999; Wang and Xu 2013). Notably, higher levels of both leaf litter traits N and P can lead to faster litter decomposition. Thus, the counteracting roles of various leaf litter traits in evergreen and deciduous broad-leaved trees likely generate this equivalent decomposition rate of leaf litter between leaf habits (Aerts et al. 2012; Ge and Xie 2017b; Hobbie 2015; Liu et al. 2016). Moreover, other studies support the central role of physical and secondary metabolites in decomposition: structural properties of leaves such as toughness or secondary compounds like polyphenols correlate with decomposition between leaf habits (Chomel et al. 2016; Hobbie 2015; Waring 2012). However, we did not incorporate the above-mentioned litter traits into our explicit analysis and thus could not single out which key litter traits that play the dominant role, considering the low data availability of litter the paucity of litter trait data for our studied broad-leaved species. Therefore, it is reasonable to expect that a trait-based approach that details the examination of the relative role of leaf litter multiple physical and chemical traits and their interactions would be promising avenues for future research to refine the mechanistic understanding of leaf habit effect on litter decomposition (Dias et al. 2017; Freschet et al. 2012; Funk et al. 2017; Powers and Tiffin 2010).

Leaf habit alters climatic effects on leaf litter decomposition

Climate, species composition (such as leaf habit), and their interaction influence leaf litter decomposition in complex ways and in combination they produce latitudinal variation in leaf litter decomposition (Cornwell et al. 2008; Funk et al. 2017; Makkonen et al. 2012). Our results revealed that across our studied region leaf litter decomposition rate of evergreen species was significantly higher than that of their deciduous counterparts (Fig. 2a). It is likely that this is associated with either the geographical or the climatic conditions across the regions of their distribution. Evergreen broad-leaved tree species are usually distributed within low-latitude regions in China, where the climate is relatively warm and wet. In contrast, deciduous species are mainly distributed at high-latitude regions where MAT and MAP are generally much lower than those at lower-latitude regions in eastern China (**Appendix** S7). The consistent relationship between the percentage of evergreen (or deciduous) species and climate along the latitudinal gradient is also indicative of the minor role leaf habit plays. The minor role species composition (leaf habit) played in leaf litter decomposition in our study did not support previous conclusions of its primary role in other forests at the regional scale and at single sites (Dorrepaal et al. 2005; Liu et al. 2016). Therefore, we suggest that the determinants of variation in leaf litter decomposition are region-specific, and for broad-leaved tree species in Eastern China, it is mainly driven by climate and less by species composition.

Here, we found that MAT was the most important determinant of leaf litter decomposition across broad-leaved tree species in Eastern China. We also found that leaf habit was only a minor contributor to variation in leaf litter decomposition, and thus a poor predictor of leaf litter decomposition in our study. These findings are consistent with the long-standing, earlier view of climate as the primary broad-scale regulator of leaf litter decomposition (Aerts 1997; Cusack et al. 2009; Waring 2012; Zhou et al. 2008), but in contrast with recent evidence which assume that other factors such as litter traits predominate decomposition process (Bradford et al. 2016; Zanne et al. 2015). However, the dominant roles of climatic variables in litter decomposition need further analysis and interactive effects between climate and litter traits on litter decomposition should also be appreciated. Litter traits may also play a dominant role but its effect is masked by the strong correlation between climate and litter decomposition rates. For example, lignin concentration could be higher in colder regions, which contributes partly to the slow decomposition rates (Aerts 1995; Berg et al. 2015; Cornwell et al. 2008). Moreover, plant functional groups such as leaf habit here could shift with climate (Dorrepaal et al. 2005; Ge and Xie 2017a), implying that climate and litter traits together become less favorable for decomposition (Aerts 1997; Bradford et al. 2016). Therefore, we cannot exclude that leaf litter developed under higher MAT will have higher litter quality, e.g. higher N and P, which may influence the decomposition rate (Berg 2014; Ge et al. 2016; Makkonen et al. 2012). These analyses indicate that the different roles of climate vs. litter traits among various decomposition studies need to be reconsidered with a new generation of experimental designs that should enable a robust evaluation of the climate-decomposition paradigm by incorporating local-scale factors such as biotic activity and litter traits into litter decomposition framework over broad geographical scales. In our present study, provided that we consider leaf habit as a proxy of leaf litter traits and that these are tightly linked to leaf litter decomposition, then our work does not support prior studies that suggest that leaf habit of tree species have a predominate effect on leaf litter decomposition

(Cornwell et al. 2008; Dorrepaal et al. 2005). Our analysis of leaf habit effects by two comparative approaches also confirmed its minor role in litter decomposition when compared to climatic effects and again highlighted leaf habit of tree species alone was not a sufficiently robust predictor of leaf litter decomposition.

The effects on leaf litter decomposition rate by climate factors, leaf habit, and their interactions have increasingly been appreciated in previous studies (Cornelissen et al. 2007; Hobbie 2015; Marklein et al. 2016). In this study, the interactive effects of climate variables and leaf habit have accounted for the largest proportion (11.39%) of the variation in leaf litter decomposition. Similar relationships between both leaf habits responses to MAT and MAP existed, but there were differential rates of change in leaf litter decomposition with climatic variables. Therefore, if our gradient analysis is a useful predictor, we expect that a future change in climate will exert idiosyncratic effects on leaf litter decomposition of different leaf habits. Our results also suggest that fundamental biosphere processes that are driven by leaf litter decomposition, such as carbon and nutrient cycling, may differ considerably between forest ecosystems with different relative abundances of leaf habits along the climatic gradients, as evidenced by the strong interaction of climate and leaf habit reported here. Therefore, such major shifts in relative abundance of these broad-leaved species of different leaf habits in response to future climate change could have large consequences for regional carbon and nutrient cycles for broad-leaved forests. Future attempts that integrate leaf habit and trait-based approaches will allow us to understand the implications of changes in leaf habit composition for decomposition and other ecosystem processes. Our findings provide compelling evidence for how litter decomposition of different leaf habits may respond to projected long-term changes in climate and underscore that we need to take this differential response into account when we attempt to further analyze potential implications of climate change for carbon and nutrient cycling via litter decomposition pathways.

Implications for ecosystem-level nutrient cycling

Our results have two aspects of important implications for nutrient cycling in broad-leaved forest ecosystems in a changing world. On the one hand, the strong interaction between climate and leaf habit and higher k values for evergreen versus deciduous species across our studied region predict that a transition from deciduous-dominated broad-leaved forests to evergreen-dominated forests, caused by climate change, will lead to faster nutrient and carbon cycling. Evergreen and deciduous broad-leaved tree species displayed different responses to climatic variables, pointing to differential climate-driven litter decomposition between evergreen-dominated and deciduous-dominated broad-leaved forests, with likely feedback to atmospheric CO_2 particularly where evergreen species replace deciduous species regionally (Ge and Xie 2017a; Ordoñez et al. 2009).

On the other hand, our findings have important consequences for plant-mediated nutrient-driven feedback to soil fertility. The role of leaf habit in plant-soil feedbacks is generally an interesting topic in ecological studies. Studies on this topic mainly come from temperate and boreal forests, with fewer studies for broad-leaved forests (Aerts 1995; Augusto et al. 2015; Mueller et al. 2012; Waring et al. 2015). Previous studies have shown that the predominance of evergreen trees coincides well with low nutrient environments, while that of deciduous species shows the opposite trend at the local scale (Aerts 1995; Ge et al. 2016; Ordoñez et al. 2009). Leaf litter decomposition is one of the central ecological processes driving plant-soil feedbacks (Aerts 1995; Hobbie 2015; Liu et al. 2016; van der Putten et al. 2016). It has been shown that nutrient release by litter decomposition is an important aspect of tree species' feedbacks to soils and plays a key role in the competitive balance of evergreen and deciduous species in forest ecosystems (Aerts 1995; Ge et al. 2016; Laughlin et al. 2015; Ordoñez et al. 2009). Previous studies have demonstrated that leaf litter decomposition is a main pathway of nutrient loss (Aerts and Chapin 1999; Hobbie 2015). Our finding identified that there were no significant differences in leaf litter decomposition rate between evergreen and deciduous broad-leaved tree species under the same environmental regimes. Therefore, it seems not reasonable to expect differences in decomposition between leaf habits alone to be predictive of plant impacts on soil fertility. Our results are further inconsistent with theories proposing a greater importance of litter decomposition rate in generating stronger plant-soil feedbacks in low fertility environments (Cortois et al. 2016; Hobbie 2015). We identified that the rate of leaf litter decomposition is not among these critical mechanisms that drive plant effects on soil fertility between evergreen and deciduous. Litter decomposition rate per se may be not a predominant pathway by which plant feedback to soil nutrient availability. Consequently, we assume that leaf litter of different leaf habits provide positive feedbacks to the soil, not through nutrient release rate by leaf litter decomposition, but via other mechanisms such as leaf litter production and leaf life span.

It is noteworthy that climate factors and leaf habit were unable to explain the major part of the variance in the decomposition rate of Chinese broad-leaved tree species in this dataset despite widespread geographical coverage. This result is similar to that of previous studies at both regional and global scales (Makkonen et al. 2012; Reichstein et al. 2014; Zhang et al. 2008) and highlights the potential importance of local scale or other biotic controls that we did not consider on leaf litter decomposition rate. Large variation in leaf litter decomposition can occur within a single site and thus further studies should focus on local-scale endogenous factors such as morphological, anatomical, and chemical construction that can influence leaf litter decomposition processes (Hättenschwiler et al. 2011; Zanne et al. 2015). Besides, leaf litter fauna or microbes not considered here may provide an additional substantial source of unexplained variation in litter decomposition. For instance, existing evidence has found that various trophic interactions between soil microbes and litter fauna can exert great control over decomposition at fine local scales, enhancing within-site heterogeneity in decomposition rate (García-Palacios et al. 2016; Makkonen et al. 2012; Zanne et al. 2015). Resolving other drivers of leaf litter decomposition for different leaf habits will require more holistic field research to better understand the impact of long-term climate conditions on carbon and nutrient dynamics of forest ecosystems. Despite these limitations, our work still provides important insight into climate-driven leaf litter decomposition over large geographical scales.

Concluding remarks

Our work comprehensively documented the variability of leaf-litter decomposition rates of broad-leaved tree species across eastern China and quantified both climate and leaf habit regulation across a broad-scale latitudinal gradient. Of the three primary factors considered to influence the geographical pattern, MAT showed the greatest influence on leaf litter decomposition and leaf habit showed the weakest. Notably, we found different climate sensitivities of leaf litter decomposition across leaf habits: leaf litter decomposition of evergreen broad-leaved tree species was more sensitive to MAT than that of the deciduous species, whereas leaf litter decomposition of the deciduous trees was more sensitive than that of the evergreen to MAP. Our findings add to a growing amount of evidence demonstrating that climate is the main driver of leaf litter decomposition over broad geographical scales. While much work in other forest ecosystems like tropical seasonal dry forests is needed to validate large-scale generalizations of this conclusion, this study represents an important step toward advancing our current knowledge of nutrient cycling via leaf litter in broad-leaved forest ecosystems and improve our ability to predict future impacts of global changes on ecosystem functioning. Our understanding of leaf habit effect on leaf litter decomposition will benefit from more standardized field experiments explicitly measuring decomposition of leaf litter with a range of functional traits along climatic gradients.

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